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RESEARCH PAPER

The distribution and diversity of insular ants: do exotic species play by different rules?

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ABSTRACT

Aim To examine the relationship between island characteristics (area, distance to the nearest continent, climate and human population size) and ant species richness, as well as the factors underlying global geographical clustering of native and exotic ant composition on islands.

Location One hundred and two islands from 20 island groups around the world.

Methods We used spatial linear models that consider the spatial structure of islands to examine patterns of ant species richness. We also performed modularity analyses to identify clusters of islands hosting a similar suite of species and constructed conditional inference trees to assess the characteristics of islands that explain the formation of these island–ant groups.

Results Island area was the best predictor of ant species richness. However, distance to the nearest continent was an important predictor of native ant species richness, as was human population size for exotic species richness. Native species appear slightly more modulated (i.e. well grouped in species assemblages that are present over a distinct cluster of islands) than are exotic species. Exotic species, while still exhibiting some modularity, tended to be widely distributed among island groups. Interestingly, ocean currents accounted for most of the variation in modularity and thus species composition for both native and exotic ant species.

Main conclusions Contrary to previous work, both native and exotic species appeared to be confined to particular island regions, and patterns in the distribution of both native and exotic species were limited by a similar suite of factors. However, the distribution of exotic ant species appeared to be more influenced by human-related variables and less structured relative to those of native ant species, perhaps due to the long-term (and increasing) influence of human-mediated dispersal that favours exotic species.

Keywords

Biodiversity, biological invasions, Hymenoptera: Formicidae, insular biogeography, invasiveness, nativeness, spatial distribution, species richness

INTRODUCTION

Oceanic islands have been test beds for biogeographical theory, at least since MacArthur & Wilson (1963, 1967) first elucidated the dynamic theory of island biogeography and Simberloff & Wilson (1969) went on to test its fundamental tenets experimentally. Indeed, over the last several decades biogeographers have taken diverse approaches to understand why some islands have more species than others. Concurrent with the increased understanding of insular biodiversity has

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been the increasing spread of exotic species among island systems, some of which may become dominant competitors (Borges *et al.*, 2006; Blackburn *et al.*, 2008; Traveset *et al.*, 2014; Whittaker *et al.*, 2014). These natural biogeographical experiments have resulted in novel combinations of native and exotic species, sometimes increasing but at other times decreasing local diversity; however, it is not yet clear what rules (or key processes) govern the structure and dynamics of island assemblages (Whittaker *et al.*, 2014).

The theory of island biogeography (MacArthur & Wilson, 1967) posits that island size and isolation drive speciation, colonization and extinction, which ultimately limit the number of indigenous species on oceanic islands. But do exotic species adhere to the principles of island biogeography theory? Or do they simply increase diversity on islands or decrease it when they are dominant competitors or predators? The size of islands and their geographical complexity influence habitat diversity, and therefore the number of species that can persist on an island. Habitat diversity affects both exotic and native species, whether endemic or not, such that islands with a high habitat diversity are likely to sustain a rich biota of both native and exotic species (Levine & D'Antonio, 1999; Stohlgren *et al.*, 2003).

Isolated islands can often have a unique native biota relative to the biota of the nearest mainland (Sadler, 1999). However, island isolation is more likely to influence collections of native species rather than exotic species, in part because the distribution and dispersal of exotic species is so closely tied to humans (Bartomeus *et al.*, 2012). Humans facilitate both the introduction (by removing the barriers that confine species to certain areas) and the establishment (by increasing propagule pressure) of exotic species (Williamson, 1996). Assemblages on islands shaped by anthropogenic forces seem to be randomly structured but biased by historical trading and human settlement (Helmus *et al.*, 2014).

Therefore, if the diversity of native species on islands is driven solely by the fundamental processes that lie at the heart of the theory of island biogeography, then the prediction would be that native species, rather than exotic species, should show stronger signals of matching between their niche requirements and the characteristics of islands because they have evolved in association with those islands. In addition to traditional island biogeography analyses of species richness, one way to test this prediction would be to ask whether native species on islands belong to distinct functional clusters (or modules), with species matching the habitat within a geographically clustered group of islands. In contrast, exotic species should exhibit a weaker match because many exotic species are dispersed by humans, with no regard to whether the niche requirements of the species match the characteristics of the island (Hui *et al.*, 2013).

Here, we use data on the occurrences of ant species on 102 islands that belong to 20 island groups around the world to: (1) examine the potential drivers of the insular species richness of native species (including both endemic and non-endemic species) and exotic ant species, and (2) identify global patterns of species composition and the processes that shape them – some in line with traditional island biogeography theory and others reflecting anthropogenic processes that potentially govern these clustered groups of native and exotic ants world-wide. Exotic ants constitute a diverse group of species that have become established across many islands world-wide. They have overcome biogeographical barriers associated with human-mediated transport pathways, and some species are responsible for causing a significant displacement of native fauna and altering the functioning of ecosystems (Rizali *et al.*, 2010; Morrison, 2014). While numerous studies have examined ant diversity on islands and archipelagos in many corners of the globe (see Appendix 1), none have elucidated the relationship between native and exotic ants globally, nor have they identified the potential drivers of such relationships. Therefore, to the best of our knowledge, ours is the first study to examine the biogeography of exotic insular ants at a global scale.

METHODS

Data

The occurrences of native and exotic ants on islands were extracted from existing literature. We limited the search to species checklists on small islands (area < 1000 km^2) and extended this by combining literature reviews with field work conducted after 1995 to increase the probability of complete sampling of all island habitats (Appendix 1). By doing so, we limited the analyses to studies where information on species presence was not only obtained from a compilation of published records but also from a recent field survey where both native and exotic species were identified. Many of the studies conducted prior to 1995 did not include field surveys and/or excluded exotic species from their lists (Morrison, 2014). Prior to our formal statistical analysis, we explored the completeness of the dataset by constructing species accumulation curves and the zeta-diversity index. Zeta diversity depicts the number of species shared by multiple sites and either declines with the number of sites exponentially, indicating stochastic assembly processes, or follows a power law, suggesting habitat differentiation among species (Hui & McGeoch, 2014).

The independent variables considered were related to environmental heterogeneity and natural isolation, but also to biotic diversity and human alteration (Appendix S1 in Supporting Information). Variables related to environmental heterogeneity were island area and climatic variables (mean annual temperature and mean annual precipitation; Hijmans *et al.*, 2005), while variables related to natural isolation were represented by longitude and latitude, distance to the nearest continent, distance to the nearest island, number of islands within a radius of 300 km and a series of biogeographical elements [such as biogeographical realm (Olson *et al.*, 2001) and ocean, ocean region and ocean current]. Variables related to biotic diversity (subfamily, tribe, generic and species richness) were derived from source publications, while human alteration was estimated based on the number of people

inhabiting each island. This last variable was included as a surrogate of the amount of trade and consequent opportunities for import and release of exotic ants (as in Blackburn *et al.*, 2008). Data on human population size, island area and ocean current or region were derived from online atlases, databases or encyclopaedias (UNEP, 2010; Encyclopædia Britannica, 2011; Ryan *et al.*, 2013; Wikimedia Foundation Inc., 2015).

Species richness analyses

We first investigated the univariate and multivariate relationships between native and exotic species richness and island characteristics using spatial linear models of the simultaneous autoregressive (SAR) model type. SAR models assume that the response at each location is a function not only of the explanatory variable but also of the values of the response at neighbouring locations (Kissling & Carl, 2008). A SAR of the error type (which assumes that the spatial autocorrelation is not fully explained by the explanatory variables) was chosen and a lag distance of $d = 1000$ km with weighted neighbourhood structure showed the best model fit and largely reduced the spatial autocorrelation from the residuals, although it did not completely eliminate it. In the multivariate analyses, we examined all possible combinations of five explanatory variables related to environmental heterogeneity (island area, mean annual temperature and mean annual precipitation), natural isolation (distance to the nearest continent) and human alteration (human population size) and chose the best ones based on the Akaike information criterion (AIC) (Burnham & Anderson, 2002). Non-climatic variables were $\log_{10}$-transformed to approximate normally distributed residuals. Statistical analyses were conducted using the R package Spdep (Bivand, 2015).

Species composition analyses

We then adopted a two-step approach to examine patterns of community composition of native and exotic ant diversity across islands. First we employed modularity analysis to identify groups of islands hosting similar suites of species to test the prediction that native species would be clustered among islands but exotic species would show no such clustering. Modularity analyses, also called compartmentalization, have been used in ecological studies to provide insights into the structure of food webs and co-distributions of species that are otherwise difficult to quantify (Olesen *et al.*, 2007; Hui *et al.*, 2013). The basic idea is that, given a network of nodes, modularity analyses partition the network nodes into groups (or modules) within which the number of within-group connections are more dense than the between-group connections and are maximized relative to random expectation (Newman & Girvan, 2004).

We generated a species × site matrix, with both species and islands treated as network nodes. The partitioning of nodes into modules was conducted by maximizing the network's modularity using simulated annealing in the Netcarto program (Guimera & Amaral, 2005). We used the *Z*-score of modularity for comparing natives with exotics, $M_Z = (M - M_N)/SD_N$, where M_N and SD_N are the average and standard deviation of modularity from 1000 random matrices with the same ranking of node degrees as the observed matrices (Guimera & Amaral, 2005). By using data from native and exotic species separately and a two-sample Welch's *t*-test for comparison, we tested whether native species were more compartmentalized among islands than were exotic species. A significant test would demonstrate that the characteristics of islands increase modularity, while anthropogenic processes (and unintentional introduction of exotic species) reduce it.

Second, we used the modules of islands for native and exotic species derived from the modularity analysis as the response variables in two separate conditional inference trees in order to address whether there were characteristics of the islands that promote modularity for native and exotic species. After examining the importance of variables by means of conditional inference forests, we identified the most influential ones using conditional inference trees. Conditional inference forests (or random forests) are a type of recursive partitioning method that first build a large number of bootstrapped trees (in our case 2000 trees) based on random samples of variables, and second identify the global effect of predictors across all trees by assessing the effect of changing the values of the nodes (Breiman, 2001). Variables are considered informative only when the value of the variable importance is above the absolute value of the lowest negative-scoring variable (Strobl *et al.*, 2009). Random forests have been shown to be extremely accurate across datasets (Caruana & Niculescu-Mizil, 2006).

On the other hand, conditional inference trees use permutation tests to evaluate the splits (branches in the tree) and do not require pruning (Hothorn *et al.*, 2006). At each split, a significance test on independence between any of the predictors and the response is performed. A split is established when the *P*-value, in our case adjusted for multiple comparisons of the same variable, is smaller than a pre-specified nominal level. The advantage of this approach compared with simple classification and regression trees lies in the effect of the statistically motivated stopping criterion 'the *P*-value', making pruning back of large initial trees unnecessary (Everitt & Hothorn, 2006). These analyses were conducted using the R package Party (Hothorn *et al.*, 2006; Strobl *et al.*, 2009) and including all independent variables (Appendix S1). Different modules of islands should reflect different drivers. The characteristics of islands – mainly related to environmental heterogeneity, natural isolation, and biotic diversity – should be the key drivers of islands' native modules, while anthropogenic forces could account for the exotic modules (Fisher, 2010).

RESULTS

Species data overview

Native ants occurred on 87 of the 102 islands. They were absent on 15 islands from the archipelagos of the South Atlantic islands, Madeira, the Cocos (Keeling) Islands, Polynesia and the Juan Fernández Islands. Exotic species were

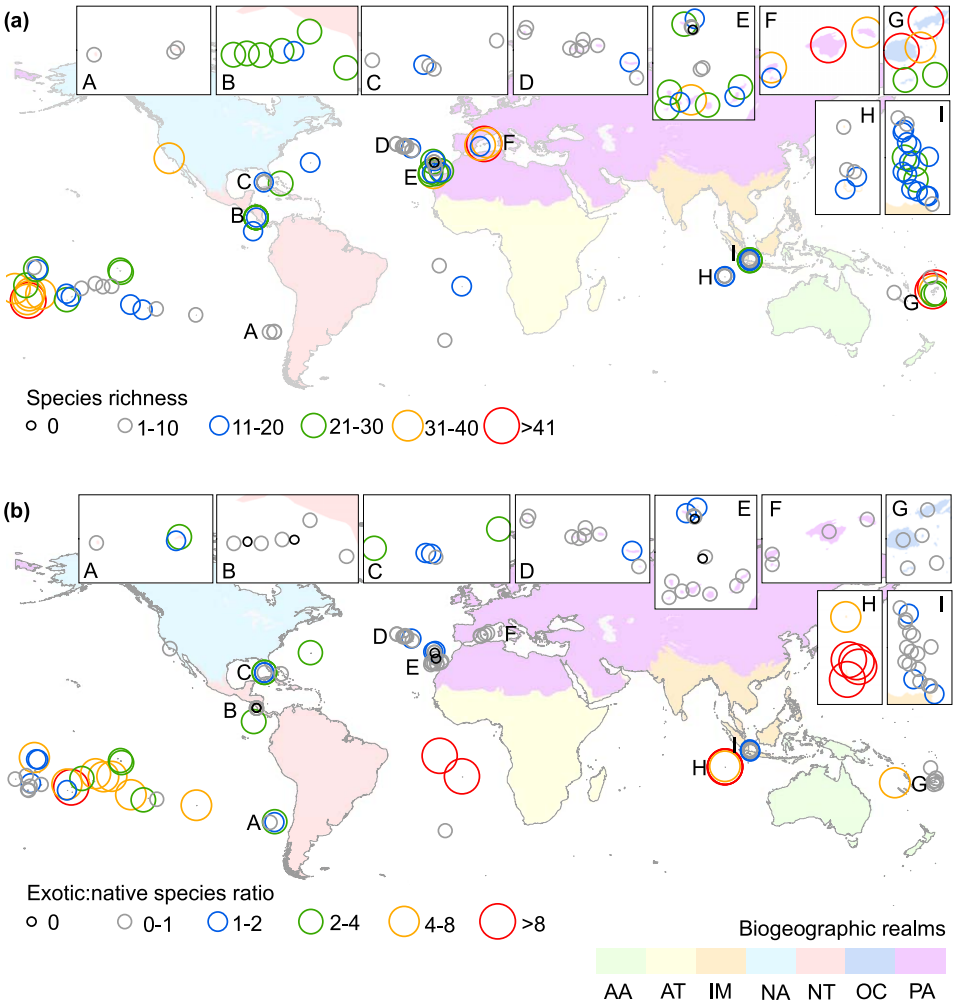

Figure 1 Distribution of ant species richness and the exotic:native species richness ratio on islands world-wide. The size and colour/size of the circles is proportional to the species numbers and ratios. The colours of the land masses show the biogeographical realms (AA, Australasia; AT, Afrotropical; IM, Indo-Malay; NA, Nearctic; NT, Neotropical; OC, Oceania; PA, Palaearctic; Olson *et al.*, 2001). The inserts represent an expanded view of areas where symbols overlap.

present on 98 islands, but were absent on only two islands from Islas Murciélago and two islands from the archipelago of Madeira. In general, there were more native species than exotic species (i.e. 308 native and 87 exotic species, with 27 species occurring as both native and exotics; Appendix S2). When we used Chao2 metric to estimate the potential diversity across all islands, the number of native species (Chao2 estimate = 603 ± 74 species; mean ± SD) was substantially higher than that of exotic species (Chao2 estimate = 125 ± 21 species; $t = 633.87$, d.f. = 200, $P < 0.0001$). These results suggest that the proportion of discovered species is higher for exotics (70%) than for native species (50%). Indeed, species accumulation curves for native species do not asymptote, even after excluding endemic species, but curves for exotic species are asymptotic (Appendix S3).

Half of the native species (48%) were found only on a single island, but the two most widely distributed species in our dataset (*Pheidole oceanica* and *Odontomachus simillimus*) occurred on 20 and 28 islands (in six and five archipelagos), respectively (Appendix S2). Exotic species follow a similar, but less pronounced, trend: a third of exotic species (37%) were found only on a single island, but 15 exotic species occurred on more than 20 islands. *Monomorium floricola* and *Paratrechina longicornis* were the most widely distributed exotic species in our dataset, present on 50 and 69 islands (in 11 and 18 archipelagos), respectively (Appendix S2). Zeta diversity followed an exponential form of decline for both native and exotic species (Appendix S3), signalling stochasticity-driven assemblage patterns.

Species richness analyses

Half of the sampled islands had more exotic species than native species. Islas Murciélagos, some Balearic islands and Santa Cruz Island had the lowest exotic:native species ratio (all were ≤0.25), while the Cocos (Keeling) Islands, Surprise Island and some Polynesian islands and South Atlantic islands had the highest exotic:native ratio (>4.5) (Figs 1 & 2a).

Univariate analyses of species richness revealed that island area, distance to the nearest continent and human population size were the most important predictors. The predictive power of island area and distance to the nearest continent was much stronger for native (where it explains 57% and

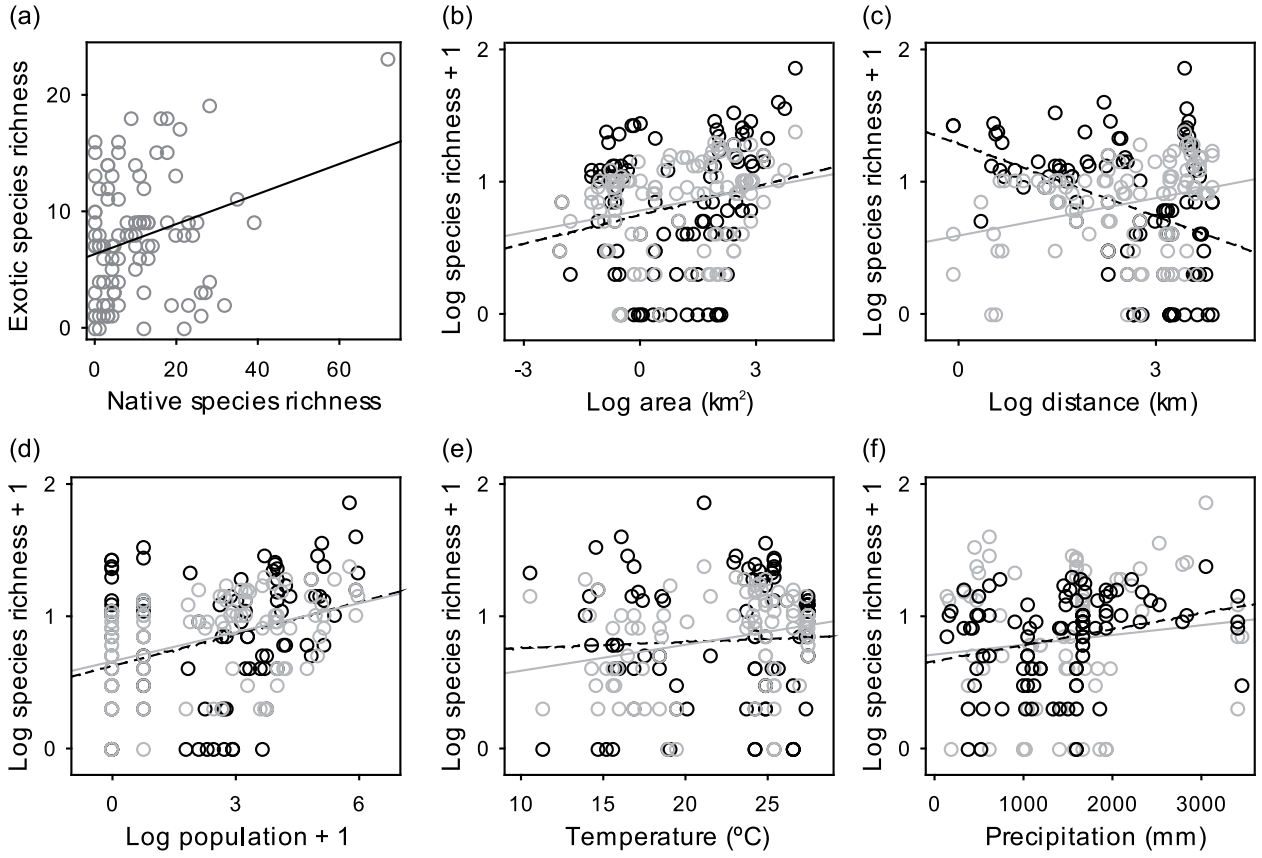

Figure 2 Relationships between island characteristics and native and exotic ant species richness. Lines show linear fits, black broken lines correspond to native species (depicted in black open circles) while grey continuous lines correspond to exotic species (grey open circles). Plot (a) shows the relationship between native and exotic species (Appendix S4). Variables in plots (b)–(f) refer to species richness [$\log_{10}(x+1)$], island area ($\log_{10}x$; km^2), distance to the nearest continent ($\log_{10}x$; km), human population size [$\log_{10}(x+1)$], mean annual temperature (x; °C) and mean annual precipitation (x; mm) (Appendix S1).

55% of variation, respectively) than for exotic species (46% and 26%, respectively), but human population size accounted for a similar amount of variance in both groups (*c.* 53%). The slope of species richness against island area and human population size was positive in both native and exotic species, but the relationship of species richness with distance to the nearest continent was negative in native species (-0.30 ± 0.07, estimate $\pm$ SE) and positive in exotics (0.09 ± 0.05) (Table 1, Fig. 2). Apart from a few divergences, this apparent difference remained robust when the native endemic and non-endemic species were considered separately (Appendices S5 & S6).

The multivariate analyses corroborated our previous results. Island area and distance to the nearest continent appeared to be the most influential variables determining native species richness, while exotic species richness appeared to be shaped by island area and human population size. In both cases, climatic variables accounted for some of the variation in richness (precipitation in the case of native species and temperature for exotic species) (Table 2). However, when examining native species separately, we found clear differences between native endemic and native non-endemic species. Native endemic species richness appears to be strongly influenced by island area, but native non-endemic species richness is accounted for mostly by distance to the nearest continent as well (Appendix S7).

Species composition analyses

The modularity analysis to examine patterns of ant species composition indicated that both native and exotic species were significantly spatially compartmentalized, with native species (nine detected modules, *Z*-test, $M_Z = 72.63$, $P < 0.001$) slightly more modulated than exotic species (seven detected modules, *Z*-test, $M_Z = 19.40$, $P < 0.001$). These differences in the degree of modularity between native and exotic species appeared to be statistically significant (Welch's $t = 309.2$, d.f. = 190.4, $P < 0.0001$), corroborating that native species are more modulated than exotic ants. These results held up even when comparing native non-endemic species with exotic species, although the degree of modularity was a little bit lower (native non-endemic species, six modules, *Z*-test, $M_Z = 39.70$, $P < 0.001$; exotic species, six modules, *Z*-test, $M_Z = 7.52$, $P < 0.001$; Welch's $t = 226.4$, d.f. = 198.0, $P < 0.0001$). The most abundant island modules for native

species were modules 2, 4 and 9 (hosting 21%, 18% and 17%, respectively), while for exotic species, modules 1, 2 and 3 (27%, 34% and 26%, respectively) were the most abundant (Appendix S8 and S9).

Table 1 Univariate spatial linear models examining the relationship between island characteristics and native and exotic ant species richness on islands world-wide. Variables refer to species richness [$\log_{10}(x+1)$], island area ($\log_{10}x$; km^2), distance to the nearest continent ($\log_{10}x$; km), human population size [$\log_{10}(x+1)$], mean annual temperature (x; °C) and mean annual precipitation (x; mm) (Appendix S1). R^2 refers to likelihood-based R^2-values after Nagelkerke (1991).

Model	Estimate	SE	Z	P	R^2
Native					
Area	0.18	0.03	5.44	<0.001	0.57
Distance	−0.30	0.07	−4.55	<0.001	0.55
Population	0.09	0.02	4.38	<0.001	0.54
Temperature	−0.04	0.02	−2.77	0.006	0.49
Precipitation	0.00	0.00	0.16	0.869	0.46
Exotic					
Area	0.18	0.02	7.16	<0.001	0.46
Distance	0.09	0.05	2.02	0.044	0.26
Population	0.12	0.01	8.27	<0.001	0.53
Temperature	0.00	0.01	0. 21	0.831	0.23
Precipitation	0.00	0.00	0.31	0.754	0.24

Conditional inference forests identified ocean current as the most informative variable for explaining the differences between modules for both native and exotic species. Other explanatory variables differed considerably in their order of importance (Appendix S10). Since we did not find any variable with a negative score, all variables were considered informative and were included in the posterior conditional inference trees. The conditional inference tree of the island modules for native species included only variables related to natural isolation (ocean current, ocean region and realm) and correctly classified 84% of the islands (Fig. 3a). Similarly, the conditional inference tree for the exotic species considered a similar set of variables (except the number of exotic subfamilies) and classified correctly an identical number of islands (84%; Fig. 3b). Models calibrated using native non-endemic versus exotic species corroborate this finding, since only ocean current appeared as the sole variable explaining differences in species modularity (Appendix S11).

The geographical distribution of modules suggests that the native modules reflect the long-term outcome of barriers limiting dispersal (Fig. 4a). Most ant assemblages in the central and southern Pacific were grouped together in module 2, while modules found in the North Atlantic differentiated the ant fauna in the east (modules 6 and 9) from the one in the west (module 5); the remaining modules presented a more localized distribution. The patterns observed in the native modules disappeared when we examined the exotic modules (Fig. 4b). The most widespread exotic modules were modules 1 and 2: module 1 distributed primarily along the Atlantic

Table 2 Multivariate spatial linear models examining the relationship between island characteristics and native and exotic ant species richness on islands world-wide. Only the best-subset models (those with $\Delta AIC < 4$) are presented, with the most parsimonious model highlighted in bold. Each row corresponds to a different model. The third and fourth columns refer to the AIC analysis, while the other columns refer to the likelihood ratio test comparing each model with the one presenting the lowest AIC. Variables refer to species richness [$\log_{10}(x+1)$], island area ($\log_{10}x$; km^2), distance to the nearest continent ($\log_{10}x$; km), human population size [$\log_{10}(x+1)$], mean annual temperature (x; °C) and mean annual precipitation (x; mm) (Appendix S1). Superscript 'M2' indicates that the log-likelihood-ratio test was calculated against the second model within the same set of models.

Model	N	AIC	ΔAIC	Log-likelihood	Likelihood ratio	d.f.	P
Native							
Area + distance + precipitation	**3**	**29.99**	**0.00**	**−8.99**			
Area + distance + temperature + precipitation	4	31.36	1.37	−8.68	0.63	1	0.43
Area + distance + population + precipitation	4	31.93	1.94	−8.97	0.06	1	0.81
Area + distance	2	32.25	2.26	−11.13	4.26	1	0.04
Area + distance + population + temperature + precipitation	5	33.32	3.33	−8.66	0.67	2	0.71
Area + distance + temperature	3	33.87	3.88	−10.94	^{M2}4.51	1	0.03
Exotic							
Area + population + temperature	**3**	**−16.35**	**0.00**	**14.18**			
Area + distance + population + temperature	4	−15.50	0.85	14.75	1.15	1	0.28
Area + population + temperature + precipitation	4	−15.12	1.23	14.56	0.77	1	0.38
Area + distance + population + temperature + precipitation	5	−14.80	1.55	15.40	2.45	2	0.29
Distance + population + temperature	3	−13.49	2.86	12.74	^{M2}4.02	1	0.05
Distance + population + temperature + precipitation	4	−13.12	3.23	13.56	1.23	1	0.27
Population + temperature	2	−12.96	3.39	11.48	5.39	1	0.02

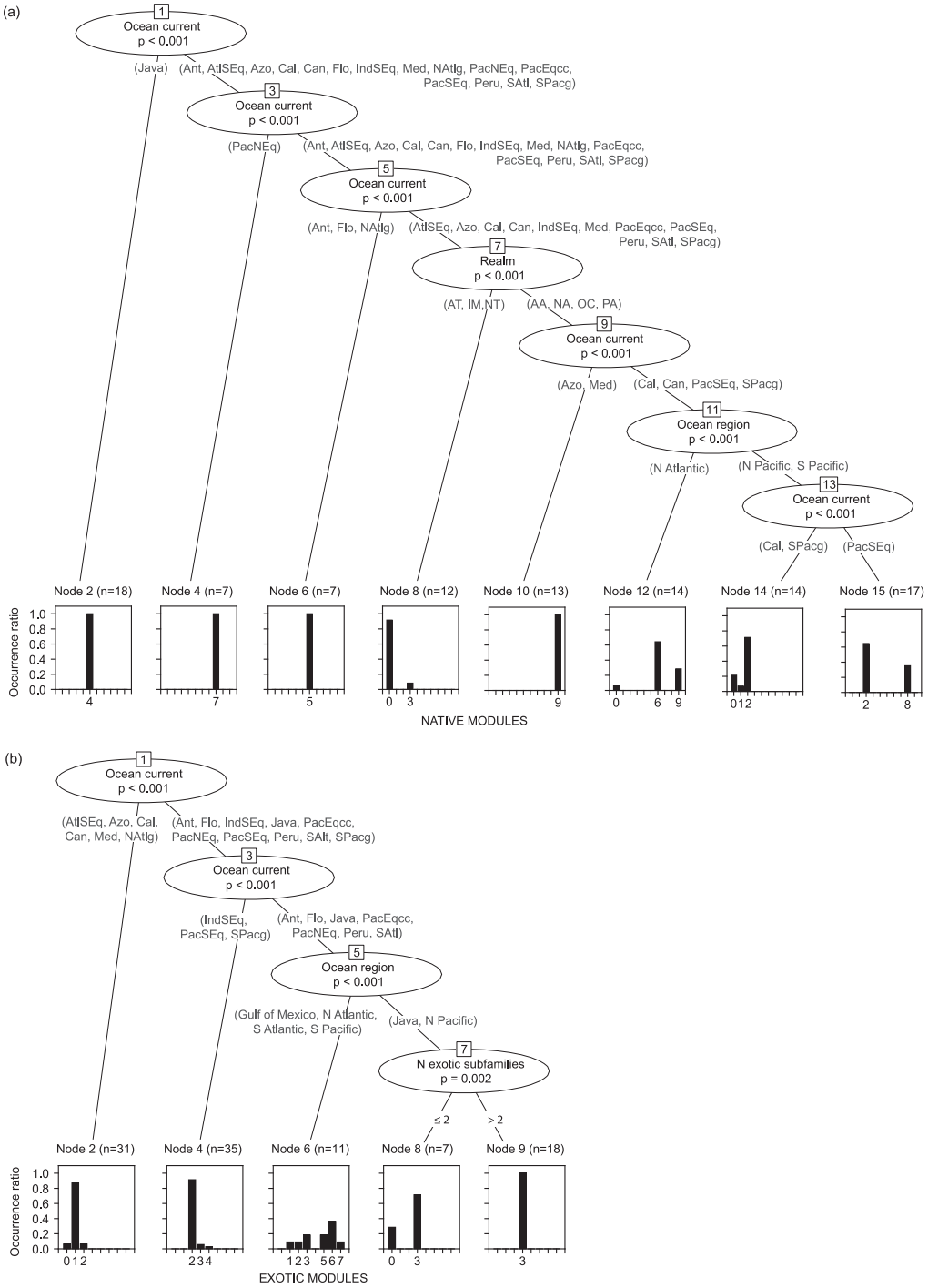

Figure 3 Conditional inference tree visualizing the distribution of (a) native and (b) exotic modules for islands (i.e. distinct clusters of islands with a certain assemblage of species) derived from a modularity analysis. Ocean current is the most relevant factor followed by biogeographical realm (realm), ocean region and number of exotic subfamilies (N exotic subfamilies). The significance value of variables chosen at each split is indicated. The bar graphs in terminal nodes show the proportion of islands in each module class. The module 0 means that the island does not have ant species. Abbreviations for ocean currents: Ant, Antilles Current; AtlSEq, Atlantic South Equatorial Current; Azo, Azores Current; Cal, California Current; Can, Canary Current; Flo, Florida Current; IndSEq, Indian South Equatorial Current; Java, Java Sea; Med, Mediterranean Sea; NAtlg, North Atlantic gyre; PacEqcc, Pacific Equatorial countercurrent; PacNEq, Pacific North Equatorial Current; PacSEq, Pacific South Equatorial Current; Peru, Peru Current; SAtl, South Atlantic Current; SPacg, South Pacific gyre. Abbreviations for biogeographical realms: AA, Australasia; AT, Afrotropical; IM, Indo-Malay; NA, Nearctic; NT, Neotropical; OC, Oceania; PA, Palaearctic.

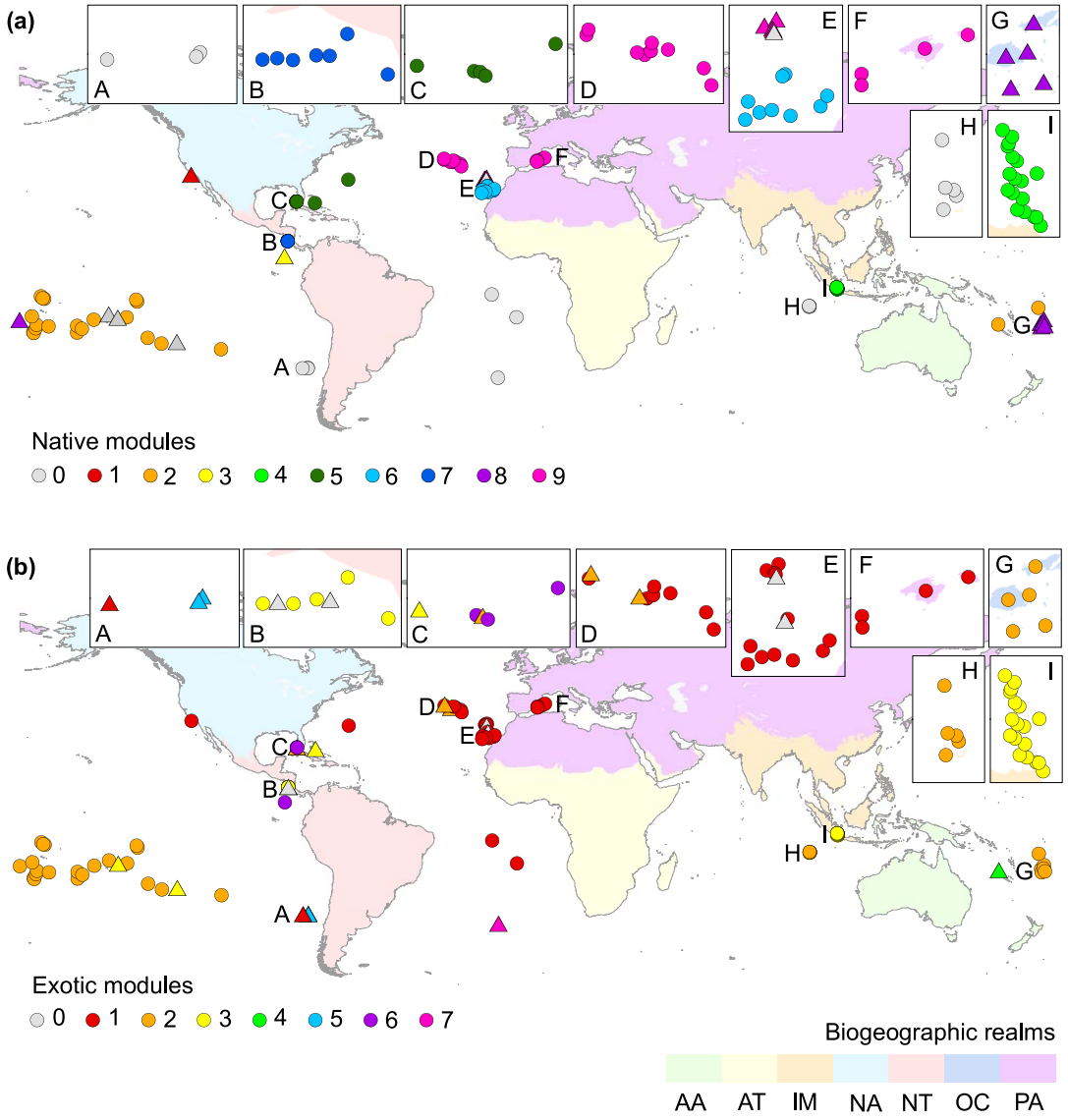

Figure 4 Distribution of (a) native and (b) exotic modules for islands (i.e. distinct clusters of islands with a certain assemblage of species) derived from a modularity analysis. The colours indicate the module assigned by the modularity analysis, while the symbols show whether the conditional inference tree grouped that particular island in a node where the majority of islands have the same module (○) or a different one (Δ). Module 0 means that the island does not have ant species. The colours of the land masses show the biogeographical realms (AA, Australasia; AT, Afrotropical; IM, Indo-Malay; NA, Nearctic; NT, Neotropical; OC, Oceania, PA, Palaearctic; Olson *et al.*, 2001). The inserts represent an expanded view of areas where symbols overlap.

Ocean and module 2 across the central and southern Pacific Ocean (Appendix S12 for a more detailed description).

DISCUSSION

Why biodiversity varies from place to place on the planet is one of the most fundamental questions in biogeography. The study of biodiversity on islands, either experimentally (Simberloff & Wilson, 1969) or observationally (Losos & Ricklefs, 2010), has illuminated many of the biogeographical processes that can shape spatial variation in biodiversity. Using data on ant biodiversity from 102 islands from 20 island groups around the world, we found that island area is the most important predictor of both native and exotic species richness, followed by distance to the nearest continent in the case of native species and human population size for exotic species. The global patterns of native and exotic species composition also appeared to be constrained to certain geographical regions by factors related to natural isolation. However, while still exhibiting some modularity, exotic ant species tended to be more widely distributed among island groups, probably due to the influence of human-mediated dispersal.

It is important to highlight, however, that these patterns depend on reliable checklists and surveys of island faunas (Appendix 1). We tried to ensure that these checklists

contained the most up-to-date information by considering only recent studies that included field sampling; even so some of them may not be complete yet and the native/exotic status of some species may still be uncertain or unknown. Moreover, because many exotic ant species are dominant competitors and displace native species (either locally or regionally) it could be the case that some native endemic and non-endemic species have become extinct and what we see today on islands around the world are homogenized ant communities dominated by only a handful of exotic, but naturalized, species. However, because our results from the analyses in which we separated native species into endemic and non-endemic species (using a reduced set of the original data, i.e. 77 islands from 18 archipelagos; see Appendix 1) present only a few divergences, we argue that our global analyses can provide initial insights into the richness and composition patterns of native and exotic ant species on oceanic islands.

Native and exotic species were present on most islands, but only a few native ants occurred on many islands, in contrast with exotic ant species that occurred on many islands. Besides these differences, the zeta-diversity indices of native and exotic species were qualitatively similar, suggesting that stochastic forces shape the distributions of both native and exotic ant species. Analyses of species richness confirmed the strong influence of island area on both native and exotic ant species. The effect of area on species diversity has received considerable attention over the years (Rosenzweig, 1995). Island area is likely to increase habitat heterogeneity, and thus ant species diversity, but it can also influence speciation, extinction and colonization (Hölldobler & Wilson, 1990; Abbott *et al.*, 2006; Fisher, 2010). However, the effect of island area is largely moulded by distance to the nearest continent. The influence of distance to the nearest continent on native ant species richness suggests that communities of native endemic and non-endemic species are shaped by two different sets of assembly processes: communities of native endemics depend more on habitat diversity, whilst native non-endemic species are shaped by dispersal (perhaps human assisted) from mainland areas as well. Contrary to native species, distance to the nearest continent does not seem to influence the richness of exotic ant species, and more isolated islands seem to harbour more exotic species than do islands that are close to continents. Such a pattern could arise if exotic ants have traits that predispose them for dispersal and establishment and they arrive on remote islands with depauperate native ant fauna (Fisher, 2010). In any case, human population seems to account for considerable variation in exotic species richness because of the role of humans as dispersal agents, facilitating the establishment of exotic species across the world (Rizali *et al.*, 2010; Morrison, 2014).

When we examined the composition patterns of insular ants, the modularity analyses indicated that the native species were slightly more modulated (i.e. separated into numerous groups of islands) than were exotic species. Natural isolation seems to be the most plausible hypothesis for explaining the higher modularity of native species. The limited dispersal ability of most native ants confines them to adjacent islands interconnected by prevailing winds and ocean currents (Fisher, 2010; Morrison, 2014). Modules 9 and 6 are quite interesting in this regard. One part of module 9 lies in the Mediterranean Sea (including the Balearic Islands) and the other in the Atlantic Ocean (including the archipelagos of Azores and Madeira), suggesting that these islands have been somewhat historically connected. Module 6, which lies between these Mediterranean and Atlantic islands (including the Canary Islands), suggests that module 9 is mainly driven by the European continent while module 6 is driven by the African continent. However, the aggregation of Atlantic islands into a single module separated from the Mediterranean ones when considering native non-endemic species alone (i.e. excluding native endemic species), suggests the idea that there is a set of species with a broad distribution in this Macaronesia region. The most widespread species are *Hypoponera eduardi*, *Lasius grandis*, *Monomorium subopacum*, *Monomorium carbonarium* and *Plagiolepis schmitzii* (Appendix S2). The rest of the modules present a more localized distribution, apart from module 2 that groups most of the islands scattered over the central and southern Pacific Ocean. The most widespread species in this region are *Technomyrmex albipes*, *Pheidole oceanica*, *Pheidole umbonata*, *Rogeria stigmatica* and *Tetramorium pacificum* in module 2, but also *Odontomachus simillimus* and *Anochetus graeffei* in module 4 (Appendix S2). Ward & Wetterer (2006) called these species 'wide-ranging Pacific natives'.

In contrast to our prediction for native ants, we expected exotic species to be little constrained by natural isolation and therefore to present a more homogeneous distribution as a consequence of human movements breaking the geographical barriers that confine taxa to certain biogeographical regions. The exotic assemblages examined in our study seem to differ among ocean currents and oceanic regions. Nevertheless, the exotic assemblages appear to be slightly less spatially structured than native ones. Module 1 is principally distributed along the Atlantic Ocean, while module 2 is distributed across the central and southern Pacific Ocean. Module 3, however, presents a more widespread distribution and cannot be localized in a specific geographical region. This apparent homogenization in the distribution of modules for exotic species is driven by the presence of a few species with a large geographical range throughout the world. Exotic ants represent only a quarter of the total pool of species, but a few of these species are present in a large number of islands. The most prominent one is *Paratrechina longicornis*, followed by *Monomorium floricola*, *Tetramorium bicarinatum, Tapinoma melanocephalum*, *Pheidole megacephala*, *Anoplolepis gracilipes*, *Cardiocondyla nuda*, *Cardiocondyla emeryi*, *Nylanderia bourbonica*, *Solenopsis geminata*, *Tetramorium smillimum*, *Linepithema humile* and *Nylanderia vaga* (Appendix S2).

Biotic interactions, at least as examined here, do not seem to influence the modular structure of these insular ant assemblages. Because we analysed changes in ant assemblages at the island level, it is difficult to detect the effect of biotic interactions operating at small scales and over a much

reduced extent (Fridley *et al.*, 2007). It is, however, relevant to note that the number of exotic subfamilies differentiates the archipelagos of Thousand Islands (Indonesia) from Islas Murciélago (Costa Rica), both in module 3, with the first presenting a higher number of subfamilies. The separation of this module could be due to the artificiality of the module, which is not restricted to a species' geographical location but groups a series of exotic species with a widespread distribution. Other variables related to environmental heterogeneity (through island area and climate), distance to the nearest land masses (such as geographical coordinates and nearest continents/islands) and human alteration (represented only by the human population size variable) do not seem to influence the compartmentalization of ant assemblages (Fig. 3). The lack of an influence of these variables in our study could be due to an incomplete sampling of the islands (Morrison, 2014), but also to the inability of these variables to capture the spatially nested structure of ant assemblages at the global scale of our analysis.

Human presence and transportation can increase the number of exotic ants on small islands (Badano *et al.*, 2005; Rizali *et al.*, 2010), but the human population size variable does not explain the similarities/differences between island modules. Following the findings of Helmus *et al.* (2014) on the influence of human movements on the biogeography of *Anolis* lizards among Caribbean islands, data on both the natural and economic isolation of islands could have provided more evidence of the effects of humans on insular ant faunas. The importance of ocean currents and regions in explaining the modularity of ant assemblages could indicate the complexity and directionality of movement of people and commodities that are responsible of these geographical patterns, acting as surrogates of both past natural and current anthropogenic isolation. The role of ocean currents and regions in explaining native assemblages could respond to the influence of long-term biogeographical processes and the movement of ants across closely related islands (Fisher, 2010), while exotic modules would be more dependent on economic factors that influence the present-day transport of humans and commodities among islands and therefore the arrival of exotic ants (Morrison, 2014).

Combining the data available on ant distributions from around the world with enhanced geographical tools allowed us to obtain a first picture of the global biogeography of exotic insular ants. It also allowed us to make a rough estimate of the geographical barriers that pose constraints on dispersal among ant assemblages, as well as identify the conditions that modulate insular ant assemblages at global scales. More field-based studies confirming whether insular ant species are native endemic, native non-endemic or exotic could refine or enhance our results. Nevertheless, our results strongly indicate that the distribution of native ants is governed by long-term ecological, biogeographical and evolutionary processes, such as natural isolation, leading to assemblages of native ants that are more modulated. In contrast, assemblages of exotic ants are less geographically constrained by natural forces but influenced by factors related to the invasion process (such as human movements) which are difficult to consider in our analysis (but see Helmus *et al.*, 2014). The number of exotic species is not expected to increase exponentially in the future, but their geographical extent may increase as a result of secondary dispersal events (Morrison, 2014). Combining data on species traits and population genetics and genomics in addition to the kinds of data we present here would provide insights into the relationships among ecological interactions, evolutionary processes, biogeographical barriers and the influence of human-aided dispersal on the distribution of ants, be they exotic or not, among islands.

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Additional references to the data sources used in this study can be found in Appendix 1.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Variables used in the species richness and compositional analyses to explain the diversity of ant species on islands world-wide.
Appendix S2 List of native and exotic ant species used in the study.
Appendix S3 Species accumulation curves and zeta diversity for native (separating endemic and non-endemic) and exotic ant species.
Appendix S4 Relationship between native and exotic ant species richness.
Appendix S5 Relationship between island characteristics and native endemic, native non-endemic and exotic ant species richness.
Appendix S6 Univariate spatial linear models examining native endemic, native non-endemic and exotic species richness.
Appendix S7 Multivariate spatial linear models examining native endemic, native non-endemic and exotic species richness.
Appendix S8 Summary results of the modularity and conditional inference tree analyses for islands.
Appendix S9 Number of islands found in each native (or native non-endemic) and exotic module.
Appendix S10 Importance of variables in explaining the modularity of islands.
Appendix S11 Conditional inference tree visualizing the distribution of native non-endemic and exotic modules for islands.
Appendix S12 Detailed description of the geographical distribution of native and exotic modules.
Appendix S13 Distribution of native non-endemic and exotic modules for islands.
Appendix S14 Distribution of nodes predicted in the conditional inference trees for native and exotic modules.
Appendix S15 Distribution of nodes predicted in the conditional inference trees for native non-endemic and exotic modules.

BIOSKETCHES

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APPENDIX 1

Data sources used in the study to determine the occurrence of native and exotic ant species on islands world-wide. Publications marked with an asterisk (*) did not have information on the endemic/non-endemic status of native ant species and were thus excluded from analyses examining the diversity of native endemic, native non-endemic and exotic species.

Ref.	Bibliographical sources by oceanic region
	ATLANTIC
1	Espadaler, X. & Bernal, V. (2003) Hormigas exóticas en las islas Canarias (Hymenoptera, Formicidae). *Vieraha*, **30**, 1–7. Espadaler, X. (2007) The ants of El Hierro (Canary Islands). *Advances in ant systematics (Hymenoptera: Formicidae): homage to E.O. Wilson – 50 years of contributions* (ed. by R.R. Snelling, B.L. Fisher and P.S. Wards), pp. 113–127. Memoirs of the American Entomological Institute, 80. American Entomological Institute, Gainesville, FL.
2	Morrison, L.W. (1998) A review of Bahamian ant (Hymenoptera: Formicidae) biogeography. *Journal of Biogeography*, **25**, 561–571
3	Wetterer, J.K. & O'Hara, R.B. (2002) Ants (Hymenoptera: Formicidae) of the Dry Tortugas, the outermost Florida Keys. *Florida Entomologist*, **85**, 303–307.
4	Wetterer, J.K. & Wetterer, A.L. (2004) Ants (Hymenoptera: Formicidae) of Bermuda. *Florida Entomologist*, **87**, 212–221.
5	Wetterer, J.K., Espadaler, X., Wetterer, A.L. & Cabral, S.G.M. (2004) Native and exotic ants of the Azores (Hymenoptera: Formicidae). *Sociobiology*, **44**, 1–20.
6	Wetterer, J.K., Espadaler, X., Wetterer, A.L., Aguin Pombo, D. & Franquinho-Aguiar, A.M. (2007a) Ants (Hymenoptera: Formicidae) of the Madeiran archipelago. *Sociobiology*, **49**, 265–297.
7	Wetterer, J.K., Espadaler, X., Ashmole, N.P., Mendel, H., Cutler, C. & Endeman, J. (2007b) Ants (Hymenoptera: Formicidae) of the South Atlantic islands of Ascension Island, St. Helena, and Tristan da Cunha. *Myrmecological News*, **10**, 29–37.
	INDIAN
8	Neville, P.J., O'Dowd, D.J. & Yen, A.L. (2008) Issues and implications for research on disturbed oceanic islands illustrated through an ant survey of the Cocos (Keeling) Islands. *Journal of Insect Conservation*, **12**, 313–323.
9*	Rizali, A., Lohman, D.J., Buchori, D., Prasetyo, L.B., Triwidodo, H., Bos, M.M., Yamane, S. & Schulze, C.H. (2010) Ant communities on small tropical islands: effects of island size and isolation are obscured by habitat disturbance and 'tramp' ant species. *Journal of Biogeography*, **37**, 229–236.
	MEDITERRANEAN
10	Gómez, K. & Espadaler, X. (2005) *La hormiga argentina (Linepithema humile) en las Islas Baleares. Listado preliminar de las hormigas de las Isla Baleares*. Documentos Técnicos de Conservación, II época, 13. Conselleria de Medi Ambient, Mallorca. Gómez, K. & Espadaler, X. (2006) Exotic ants (Hymenoptera: Formicidae) in the Balearic Islands. *Myremcological News*, **8**, 225–233.
	PACIFIC
11	Abbott, K.L., Sarty, M. & Lester, P.J. (2006) The ants of Tokelau. *New Zealand Journal of Zoology*, **33**, 157–164.
12	Cerda, X., Angulo, E., Caut, S. & Courchamp, F. (2012) Ant community structure on a small Pacific island: only one native species living with the invaders. *Biological Invasions*, **14**, 323–339.
13	Ingram, K.K., Bernardello, G., Cover, S. & Wilson, E.O. (2006) The ants of the Juan Fernandez Islands: genesis of an invasive fauna. *Biological Invasions*, **8**, 383–387.
14*	Jacobs, J.M., Longino, J.T. & Joyce, F.J. (2011) Ants of the Islas Murcielago: an inventory of the ants on tropical dry forest islands in northwest Costa Rica. *Tropical Conservation Science*, **4**, 149–171.
15	Morrison, L.W. (1997) Polynesian ant (Hymenoptera: Formicidae) species richness and distribution: a regional study. *Acta Oecologica*, **18**, 685–695.
16	Solomon, S.E. & Mikheyev, A.S. (2005) The ant (Hymenoptera: Formicidae) fauna of Cocos Island, Costa Rica. *Florida Entomologist*, **88**, 415–423.
17	Ward, D.F. & Wetterer, J.K. (2006) Checklist of the ants of Fiji (Hymenoptera: Formicidae). *Bishop Museum Occasional Papers*, **85**, 23–47.
18	Wetterer, J.K. (2002) Ants of Tonga. *Pacific Science*, **56**, 125–135.
19	Wetterer, J.K. (2006) Ants (Hymenoptera: Formicidae) of Niue, Polynesia. *Pacific Science*, **60**, 413–416.
20	Wetterer, J.K., Ward, P.S., Wetterer, A.L., Longino, J.T., Trager, J.C. & Miller, S.E. (2000) Ants (Hymenoptera: Formicidae) of Santa Cruz Island, California. *Bulletin of the Southern California Academy of Sciences*, **99**, 25–30.